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Population Viability of Avian Endangered Species: the PVAvES Program

Robert H. Melton, Leslie A. Jetté, Timothy J. Hayden, and Timothy A. Beaty

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Foreword

This study was conducted for Headquarters, Department of the Army, Assistant Chief of Staff (Installation Management) (ACS(IM)) under 62720A896, "Environmental Quality Technology," Work Unit TD9, "Threshold Impact of Maneuver Training." The technical monitor was Dr. Victor Diersing, DAIM-ED-N.

The work was performed by the Ecological Processes Branch (CN-N) of the Installations Division (CN), Construction Engineering Research Laboratory (CERL). The CERL Principal Investigator was Timothy J. Hayden. Timothy A. Beaty is employed at the Fish and Wildlife Branch, Directorate of Public Works, Fort Stewart, GA. The technical editor was Gloria J. Wienke, Information Technology Laboratory. Steve Hodapp is Chief, CEERD-CN-N, and Dr. John T. Bandy is Chief, CEERD-CN. The associated Technical Director was Dr. William D. Severinghaus. The Acting Director of CERL is William Goran.

CERL is an element of the U.S. Army Engineer Research and Development Center (ERDC), U.S. Army Corps of Engineers. The Director of ERDC is Dr. James R. Houston and the Commander is COL James S. Weller.

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1 Introduction

Background

A complex, and somewhat paradoxical, relationship exists between United States military installations and endangered species. Military activities can significantly alter habitats. Nevertheless, large tracts of military landscapes are essentially undisturbed, or disturbed in ways that allow the natural succession of native plant species. Thus, military lands often support threatened and/or endangered species by providing sizable vestiges of natural habitat within a given ecological region. This fortuitous conservation function of military lands causes potential problems for the U. S. military. Restrictions on military activities, imposed on behalf of threatened and endangered species, can conflict with accomplishment of the military training mission. On the other hand, failure to assure adequate protection for threatened and endangered species can lead to violation of the Endangered Species Act of 1973, resulting in costly disruption of military operations. As a result, U. S. Army Regulation (AR 200-3) requires each Army installation that has endangered species to prepare an Endangered Species Management Plan (ESMP). Protection of resident threatened and endangered species requires cooperation with other Federal agencies (in particular, the U. S. Fish and Wildlife Service [USFWS]).

Increased emphasis on conservation and protection of endangered species motivates the active management of endangered populations and their resources on military lands, with the goal of decreasing the likelihood of population extinction (i.e., to increase population viability). Toward achievement of this objective, it is useful, if not imperative, to be able to assess the current viability of the population, and to estimate the consequences of potential disturbances (both man-made and natural) to population viability. A rich literature on this topic, termed "population viability analysis" (PVA) has developed over the past decade (see Taylor 1995, Ludwig 1999, Bessinger and Westphal 1998, Groom and Pascual 1998, and White 2000 for reviews). Several off-the-shelf computer programs for calculating the probability of extinction of a population over a given time period are available.

A major shortcoming of PVA is that the output statistics typically estimated, such as the probability of extinction within 100 years, are highly sensitive to the

values input to the PVA model. These input values include estimates of demographic parameters such as survival rates and fecundities. These estimated demographic parameters have inherent uncertainty due to finite sample size. Sampling variance, as opposed to temporal parameter variance due to environmental fluctuations, is typically not accounted for in PVA predictions. Such sampling variance can have quite large effects on model output.

Another less commonly noted problem with PVAs based on survival and fecundity estimates is encountered when random values generated, to simulate environmental variation in naturally bounded parameters such as survival rate (which can take values only between 0 and 1), are artificially truncated. If values generated from a normal distribution are used to simulate variation in such parameters, the values must be truncated in some fashion when generated values transgress the natural boundaries. Typically, for survival rates, values greater than 1 are set to equal 1, and values less than 0 set equal to 0. Unfortunately, this implies that if the mean and temporal standard deviation of, for example, adult female survival rate are entered as inputs to the model, there is no guarantee that those input values for mean and standard deviation are the values that the program is actually using. A similar effect can occur when simulating fecundity estimates with natural boundaries, such as 0 and a maximum fecundity value.

Military land mangers do not have a population viability program, applicable to endangered species on military lands, that addresses the above criticisms. Managers need a program that can (1) generate plausible confidence intervals for its output population viability statistics given sampling error in the input demographic parameters, and (2) use the input demographic parameter values (means and standard deviations) as entered, without bias, regardless of proximity of values to their natural limits.

Objective

The objective of this research was to create a computer program, PVAvES (Population Viability for Avian Endangered Species) version 1.0, designed to assess the population viability status of endangered species on U. S. Army lands. It also facilitates the comparison of alternative scenarios based on different assumptions about the effects of disturbance, either natural or due to military activities (e.g., training methods and protocols), and also facilitates comparing the potential effects of different management options. The program represents an improvement over existing off-the-shelf PVA software, in that it utilizes, rather than ignores, the effects of input parameter sampling error to calculate output

statistics with statisical confidence intervals. It also makes use, in its simulation of temporal and sampling parameter variability, of random variables derived from the standard beta distribution, rather than the normal distribution. This allows simulated random survival and fecundity parameters to take values within specified limits, without truncation, and without bias of the input parameter values.

Approach

PVAvES was written in ANSI C programming language; it performs a Monte Carlo analysis of population viability. It essentially employs a female-based, stochastic single-population Leslie/Lefkovitch matrix projection model such as described in Burgman, Ferson, and Akçakaya (1993), incorporating demographic, environmental, and catastrophic uncertainty, as defined in Shaffer (1987). Note that in the following sections, asterisks (*) denote bootstrap samples and bootstrap parameter estimates, in notation following that of Efron and Tibshirani (1993).

Scope

As the name suggests, program PVAvES is designed primarily to use parameter estimates from demographic data typically collected on avian species (birds). More specifically, the program was designed to assist in the management of the endangered species *Picoides borealis*, the Red-cockaded Woodpecker (RCW), on Fort Stewart, GA, and to help predict the potential effects of disturbance due to military activities.

While the immediate scope of this report is a single endangered species population on one Army installation, the parameter inputs to model PVAvES use demographic data typically collected for many avian species (and some non-avian ones). The model is readily applicable to other RCW populations on other military installations, and is potentially a useful PVA tool for many other species in many different situations. The model applies only to single populations of single species, and is thus not suitable for assessing disturbance effects on ecological communities, or the viability of groups of populations (metapopulations).

The present report will not attempt to analyze the effects of specific military activities. Such an analysis for the Fort Stewart RCW population is presently in preparation. Rather, in this demonstration, the model will be used to answer a basic question pertinent to all future analyses related to Fort Stewart (and other

coastal RCW populations): Do hurricanes pose a substantial threat to the viability of the RCW population on the installation, or, put another way, should the potential catastrophic effects of hurricanes be included regularly in all PVAs of the RCW on Fort Stewart?

Mode of Technology Transfer

Information in this report will be provided to the U. S. Fish and Wildlife Service, Fort Stewart, and The U.S. Army Forces Command (FORSCOM), Training and Doctrine Command (TRADOC), and to all installations with resident Red-cockaded woodpecker populations. Program PVAvES is available from the authors on request.

2 The PVAvES Program

Overview of Algorithm

Program PVAvES uses a modified form of the parametric bootstrap algorithm (Efron and Tibshirani 1993) to generate outputs based on estimated input parameters. Figure 1 presents a summary of the algorithm used in PVAvES for generating estimates of population viability parameters, while Tables 1 and 2, respectively, present descriptions of the model inputs, and its main internal variables and outputs. The heart of the model is a population viability random variable generating function, g(ϕ), which takes as its argument a vector of estimated input parameter values, ϕ, which reflect demographic attributes of the population and its environment. The components of ϕ are presented in Table 1, along with references to the corresponding input value numbers in the formatted input file, from which PVAvES reads its input data (see Appendix B for an example input file).

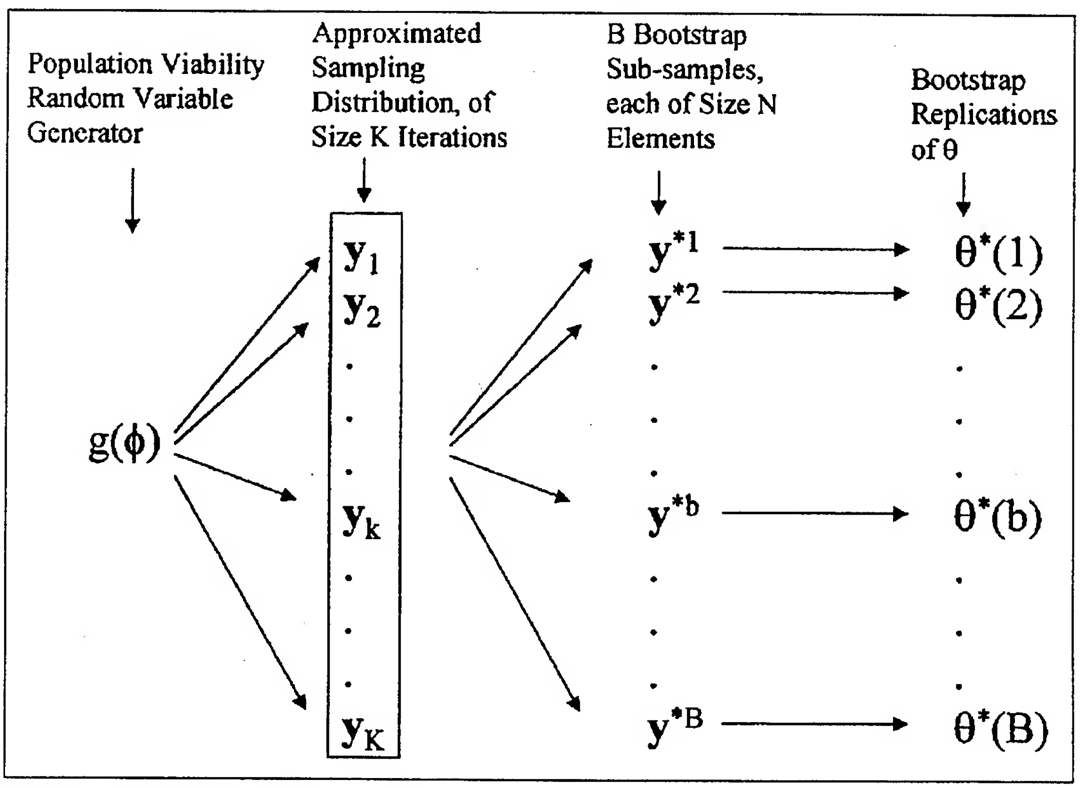

Figure 1. PVAvES algorithm summary.

Table 1. Symbols for component parameters.

Input Parameter	Parameter	Non-Temporal (Sampling) Standard Deviation	Temporal Standard Deviation	Input ID Number in formatted Input File
Effective Sample Size (of demographic data set) = Size of Bootstrap Sub-samples	N			3
Number of Bootstrap Sub-samples (taken from ASD)	B			4
Size of Approximated Sampling Distribution	K			5
Initial Population Size (breeding females)	N_0			7
Maximum Population Carrying Capacity (breeding females)	N_{max}			8
Pseudoextinction Threshold (nesting females)	N_{ext}			9
Target Population after 100 Years (nesting females)	N_{trg}			10
Probability of Nest Success	P	σ_P	τ_P	11, 12, 13
Total Number of Fledglings per Successful Nest	F	σ_F	τ_F	14, 15, 16
Maximum Number of Fledglings per Nest	F_{max}			17
Probability of a Fledgling being Female	P_f			18
Survival Rate of Female Fledgling (to next breeding season)	S_a	σ_a	τ_a	19, 20, 21
Annual Survival Rate of Adult Females	S_j	σ_j	τ_j	22, 23, 24
Rate of Immigration into Population	I			26
Regeneration Time of Carrying Capacity (years) from 1% to 99% of N_{max}	T_r			
Catastrophe Parameters (Levels x = 1 through 10):				
Rate of occurrence (annual)	ρ_x			30, 33, 36, .. 51, 54, 57
Proportional Reduction of Survival Rates	β_x			31, 34, 37, .. 52, 55, 58
Proportional Reduction of Carrying Capacity	γ_x			32, 35, 38, .. 53, 56, 59

During execution of PVAvES, the function $g(\phi)$ is iterated a large number, K, times. Each individual iteration, k, of the function g produces, as output, a random variable vector y_k, composed of 5 population viability statistics, as defined in Table 2d. Each y_k is the result of 1000 replicate population runs, each of which uses a maximum of 100 time steps (years). The resulting set of K random replicates of vector y_k comprises what is here termed the Approximated Sampling Distribution (ASD) of population viability, given input parameters ϕ.

Table 2. Parameters and variables used in the population viability model.

(a) Counter Variables:	
k = 1 through K	Iteration of the population algorithm generating the Approximate Sampling Distribution (ASD).
b = 1 through B	Bootstrap sub-sample of the ASD.
n = 1 through N	Element drawn from the ASD within each bootstrap sub-sample.
j = 1 through 1000	Population Runs within each iteration (k) of the PV Random Variable Generator g(p)
t = 1 through 100	Time step, within each population run (j) of each iteration (k).
(b) Parameters values that vary stochastically among samples and/or time steps:	
P_{kjt}	Probability of a female producing a successful (at least one fledgling) nest.
F_{kjt}	Seasonal fecundity (fledglings, both sexes) of females with successful nests.
$S_{j,\,kjt}$	Survival probability of juvenile (fledgling) females to the following year.
$S_{a,\,kjt}$	Survival probability of adult (after-hatch-year) females to the following year.
(c) Internal variables that varied at each time step, within each iteration and population run:	
$N_{ceil,\,kjt}$	Population ceiling carrying capacity in iteration i, run j, time step t.
$N_{sy,\,kjt}$	Number of second-year females.
$N_{hy,\,kjt}$	Number of female hatch year fledglings produced.
$N_{hyfldg,\,kjt}$	Number of fledglings (both sexes).
$N_{succnest,\,kjt}$	Number of successful nests.
$N_{asy,\,kjt}$	Number of older (after-second-year) females.
$N_{a,\,kjt}$	Number of adult females.
(d) Components of output vector $\mathbf{y}_k$ (for each iteration k of the Approximated Sampling Distribution):	
λ_k	Potential per capita rate of population increase, based on demographic parameters.
$P_{E100,\,k}$	Probability of pseudoextinction within 100 years.
$P_{E20,\,k}$	Probability of pseudoextinction within 20 years.
$P_{E10,\,k}$	Probability of pseudoextinction within 10 years.
$P_{N \geq target,\,k}$	Probability of seeing a breeding female population greater than or equal to N_{trg} at the end of 100 years.
(e) Components of output population viability parameter vector $\theta^*(b)$ (for each bootstrap sub-sample b):	
$\lambda^*(b)$	Mean potential per capita rate of population increase.
$P_{vuln}^*(b)$	Probability that the population is classed as VULNERABLE (see text).
$P_{endg}^*(b)$	Probability that the population is classed as ENDANGERED (see text).
$P_{crit}^*(b)$	Probability that the population is classed as CRITICAL (see text).
$P_{opt}^*(b)$	Probability that the likelihood of target population achievement after 100 years is OPTIMISTIC (see text).
$P_{btev}^*(b)$	Probability that the likelihood of target population achievement after 100 years is BETTER THAN EVEN CHANCE (see text section 2.2).
$P_{pess}^*(b)$	Probability that the likelihood of target population achievement after 100 years is PESSIMISTIC (see text).

After construction of the ASD, a series of B bootstrap sub-samples, y^{*b}, are drawn (with replacement) from the ASD. Each bootstrap sub-sample is of size N, the effective sample size of the data set from which the demographic parameter estimates were derived (the determination of effective sample size is discussed further in the demonstration analysis in Chapter 3). A vector of output population viability parameters, $\theta^*(b)$, is then calculated from each bootstrap sub-sample.

Once the B replicates of $\theta^*(b)$ are calculated, the bootstrap estimate for output parameter vector θ is estimated as:

$$\theta^*(\cdot) = \sum_{b=1}^{B} \theta^*(b) / B$$

and the bootstrap standard error (BSE) of θ is estimated as:

$$BSE(\theta) = \sqrt{\left\{\sum_{b=1}^{B} [\theta^*(b) - \theta^*(\cdot)]^2 / (B-1)\right\}}$$

Percentile confidence intervals, and BCa (bias-corrected, accelerated) percentile confidence intervals are calculated for each component parameter of θ using the formulae given in Efron and Tibshirani (1993). These bootstrap estimates, bootstrap standard errors, and confidence intervals are printed to an output data file, and the program terminates. Details of the algorithms followed by PVAvES are provided in Appendix A.

Details of the algorithms followed by PVAvES are provided in Appendix A. Algorithms used for random number and beta random variable generators were those implemented in program RANLIB.C, written by Barry W. Brown and James Lovato of the University of Texas. Algorithms for calculation of normal distribution statistics were those implemented in program DCDFLIB.C, written by Barry W. Brown, James Lovato, and Kathy Russel of the University of Texas. Both programs are available as public domain software at the NETLIB repository at the University of Tennessee at Knoxville and Oak Ridge National Laboratory, at http://www.netlib.org.

Definitions of Population Viability Terms Used in PVAvES

The rate of population increase, λ, is defined as the potential per capita rate of increase implied by the input parameters relating to survival and reproduction, in the absence of density-dependent population regulation or the effects of catastrophes, and in the absence of immigration or losses through harvest. Values of $\lambda < 1$ indicate average survival or fecundity rates insufficient to avoid certain eventual extinction. However, values of $\lambda \geq 1$, which indicate vital rates favorable to population survival, do not necessarily imply assured population persistence. This is due to the presence of a ceiling on population size, combined with the effects of demographic, environmental, and catastrophic stochasticity.

Military criteria defining levels of population extinction risk for threatened and endangered species on military lands do not exist at present. The following extinction risk class definitions used in PVAvES are based on the IUCN* extinction risk criteria relating to quantitative population viability analyses, as proposed in Mace and Stuart (1994) and in IUCN (1994).

VULNERABLE:	The probability of pseudoextinction within 100 years $\geq$ 0.1
ENDANGERED:	The probability of pseudoextinction within 20 years $\geq$ 0.2
CRITICAL:	The probability of pseudoextinction within 10 years $\geq$ 0.5

where pseudoextinction is defined as the event when the population size falls below the pseudoextinction threshold, N_{ext}.

The following further definitions relate to the prospects for observing a breeding female population equal to or exceeding the target population value, N_{trg}, at the end of 100 years, denoted $P_{N \geq target}$.

OPTIMISTIC:	$P_{N \geq target} > 0.9$
BETTER THAN EVEN CHANCE:	$P_{N \geq target} > 0.5$
PESSIMISTIC:	$P_{N \geq target} < 0.1$

Note that, based on these definitions, the six probabilistic output parameters in Table 2e (all except λ) actually express probabilities that the population falls into the categories defined above, i.e., probabilities of probabilities.

* IUCN is the International Union for Conservation of Nature and Natural Resources, which is also known as the World Conservation Union.

Use of the output parameters in Table 2e was deemed more appropriate than reporting the means or medians of $P_{E10,k}$, $P_{E20,k}$, $P_{E100,k}$, or $P_{N \geq target,k}$ as output parameters. The distributions of these four parameters among iterations of function g tended to be either highly positively or negatively skewed, or highly bimodal. Thus, their mean and median values among iterations did not reflect any actual central tendencies in their distributions.

3 Demonstration: The Red-cockaded Woodpecker on Fort Stewart

Demonstration Objective

This chapter discusses a PVA of the RCW on Fort Stewart, GA, conducted as an adjunct to the ongoing development of the Fort Stewart ESMP. The demonstration attempts to provide answers to the following questions: (1) Which IUCN extinction risk class best describes the Fort Stewart RCW population under the present management strategy, and how much uncertainty is there in this classification? (2) How likely is the RCW population, under the present management plan, to achieve a population at least as large as the Fish and Wildlife Service guideline of 250 breeding pairs over the long term? (3) Does inclusion of hurricane catastrophes into the model substantially alter the answers to questions (1) and (2)?

Materials and Methods

The Fort Stewart RCW Population

Picoides borealis, or the Red-cockaded Woodpecker, is an endangered species, endemic in the southeastern United States, and found on many regional U. S. Army installations in substantial numbers. The RCW inhabits stands of old-growth pine forest, cleared of hardwood understory by intermittent fires, that contain a high percentage of pine trees greater than 80 years old. It builds its nest cavities in older live pines, which are frequently infected with the red-heart fungus (*Fomes pini*; Jackson 1995), promoting nest cavity excavation. Extensive clearing of old-growth forests in recent decades has severely reduced and fragmented the RCW's original habitat (Jackson 1994). The species was placed on the Federal list of endangered species in 1970, and a recovery plan for the species is in effect (U. S. Fish and Wildlife Service 1985).

Fort Stewart is located in the Atlantic Coastal Plain region of Georgia, approximately 35 miles (56 km) from the Atlantic coast. This location puts the installation at substantial risk from hurricanes (Hooper and McAdie 1995). Manage-

ment practices on the installation include nest monitoring, bird banding, control of mid-story hardwood encroachment into RCW habitat, and population enhancement through the creation of artificial nest cavities in suitably old trees, at a rate proportional with observed population growth (not exceeding 10 percent per year).

Maximum RCW Carrying Capacity

The installation has an estimated 142,854 acres (57,811 ha) of suitable and potentially suitable RCW habitat, based on the premise that all upland forested areas (other than those designated for hardwood management) are manageable as RCW habitat (Fort Stewart draft multi-species ESMP). The present Fort Stewart RCW management policy attempts to increase the RCW population up to its carrying capacity, estimated to be 714 active RCW colonies, assuming an average of 200 acres (90 ha) per colony (Fort Stewart Endangered Species Management Plan, February 4 1999 draft). This converts to a carrying capacity of approximately 506 breeding females (Appendix B, input 8), given the average ratio of active colonies to breeding females between 1995 and 1998 (= .706).

Long-term Target Population Size

A target value for a viable RCW population is operationally defined as 250 breeding pairs in the RCW recovery plan (U. S. Fish and Wildlife Service 1985), based on theoretical considerations in Franklin (1980). This value was entered as the value for P_{trg}, the target population to equal or exceed at the end of 100 years (Appendix B, input 10).

Pseudoextinction Threshold

Following the recommendation of Bessinger and Westphal (1998), a pseudoextinction threshold, N_{ext}, was used as a precautionary measure to compensate for potential "extinction vortex" phenomena, such as allee effects and inbreeding depression, that could disproportionately increase the likelihood of extinction at very low population densities (Gilpin and Soulé 1986). The value of N_{ext} was arbitrarily set to equal 5 breeding females in the present analysis (Appendix B, input 9). Assuming that the ratio of effective to actual population size (N_e/N) is approximately .65-.80 in the RCW (Reed et al. 1993), this is equivalent to 3 or 4 effective breeding pairs.

Demographic Parameter Estimates

Studies of the Red-cockaded Woodpecker began on Fort Stewart in 1994. Between December 1994 and December 1998, a total of 881 RCW individuals were banded, including 253 adults (115 female, 138 male) and 628 juveniles (244 female, 243 male, 141 unknown-sex). As of 1998, there were 268 total RCW colonies recorded: 190 of which were active (evidence of birds in residence). Of these active colonies, 140 nested in 1998; this number is taken to be the starting breeding female population in this analysis (Appendix B, input 7).

Detailed reproductive data were collected on a randomly chosen sample of 67 colony sites, which have been monitored since 1995 (Fort Stewart Endangered Species Management Plan, February 4 1999 draft). Data on the resighting of banded individuals were most consistently taken within this subset of colony sites, while resightings at other locations were more opportunistic. Input life-history parameter values (Appendix B, inputs 11-24) were based on population and vital rate (survival and fecundity) data collected on the RCW female population at Fort Stewart from 1995 through 1998. Hatch-year and adult female annual survival rates, and their standard errors, were estimated from banding data using the program JOLLYAGE (Pollock et al. 1990). Limitations of sample size permitted survival rate estimates from1995 and 1996 only. Nest productivity parameters represent data from years 1995 through 1998.

Variances for the annual survival rates of fledglings and adult females, the probability of nest success, and the number of fledglings per successful nest, were partitioned into temporal and non-temporal (primarily sampling) variance components (Table 1). This was accomplished using the methods described in Gould and Nichols (1998) for survival and methods adapted from Stewart-Oaten, Murdoch, and Walde (1995) for fecundities. During model operation, the sampling variances were applied to the variation of mean parameter values among iterations of the model. The temporal variances were applied to the variation of vital rates around their mean values among time steps within each population run (see Appendix A).

Effective Sample Size

The effective sample size N (size of the bootstrap sub-samples) should represent the size of the data set from which the survival- and fecundity-related parameter estimates were derived. Determination of the appropriate value for N is problematical. Candidates for N based on the banding/survival data include the total number of releases (or resightings) of RCW females from each year, or the total number of unique females released over the course of the study (1995 through

1998). However, reliable data on nest success and fecundity were available for only a subset of these females, many of which were not observed in a given year.

For the present analysis, the value of N was set to equal 154, the total number of observed nesting events during the 4-year interval (Appendix B, input 3). The analysis was subsequently repeated using a more conservative estimate for N of 103 breeding females. This was the total number of unique individual adult females observed attempting to breed at least once on the 67 colony sites monitored during years 1995-1998. The results of this re-analysis differed in no substantial way from the results presented in this paper, and are not presented here.

Hurricane Catastrophe Scenarios

Parameter input values for the recurrence rates, ρ_x, of catastrophe levels x = 1-3 (Appendix B, inputs 30, 33, 36) were based on the estimated recurrence rates of Saffir-Simpson category I, II, and III strength hurricanes for Ft. Stewart (Hooper and McAdie 1995). The values for proportion reduction of survival rates and carrying capacity by Category III hurricanes (β_3 =.68,γ_3 = .59 Appendix B, inputs 37-38) were taken directly from the documented effects of Hurricane Hugo on the Francis Marion National Forest in North Carolina and its RCW population (Watson et al. 1995), since Hugo was a category III hurricane when it hit the population. In the absence of better information, comparable parameter values for categories I and II hurricanes (β_1, γ_1; β_2, γ_2: Appendix B, inputs 31-32; 34-35) were estimated from the values of β_3 and γ_3. This was done by assuming that their values varied in direct proportion to the square of the threshold maximum sustained wind speeds for each category as given in Hooper and McAdie (1995), i.e. varied in proportion to the wind's kinetic energy. These threshold maximum wind speeds defining hurricane classes are 74 mph for category I, 96 mph for category II, and 111 mph for category III hurricanes. As an example calculation, the survival reduction parameter $\beta_1 = \beta_3 (W_1/W_3)^2 = 0.63(74/111)^2 = 0.28$. All parameter values for catastrophe levels 4-10 (Appendix B, inputs 39-59) were set equal to 0.

The regeneration time for carrying capacity, was estimated to be 100 years. This estimate was based on the approximate time it takes for longleaf pines to grow from seedlings to mature trees suitable for RCW cavity building. In practice, trees sufficiently large for use as RCW cavity trees (particularly if using artificial cavity inserts) may be grown in as few as 60 years. However, 100 years was used as a conservative estimate of regeneration time, allowing for some variability in regenerative growth rates among trees and among training areas.

To assess the importance of hurricanes to the viability of the Fort Stewart RCW population, the model was run under two hypothetical hurricane catastrophe scenarios. These scenarios were:

1. "Hurricanes Absent": Probability of hurricanes of any strength = 0. Population fluctuations are affected only by "normal" demographic and environmental temporal stochasticity of vital rates.
2. "Hurricanes Present": Hurricanes of all strength categories had non-zero probabilities. They reduced fledgling and adult survival rates by specified percentages only during the time step (year) in which they occurred. Hurricane hits were independent, and multiple hits per year of any category combination were possible. Each hurricane hit also decreased the population carrying capacity from its current value, after which carrying capacity increased logistically toward its maximum value until the next year in which a hurricane occurred.

The two catastrophe scenarios were run using identical input files, except for the value of the parameter to toggle the presence of catastrophes (Appendix B, input 27).

Computational Facilities

All calculations were processed using an Intel Celeron 300A computer system from Ikon Technologies, Inc.

4 Results and Discussion

Results

Rate of Increase

Table 3 shows that the potential per capita rates of population increase, λ, were identical in the two hurricane catastrophe scenarios. This is expected, since the demographic parameters input to the two scenarios were identical, except for those related to catastrophes. The value $\lambda = 1.040\ yr^{-1}$ is significantly different from 1 (the value for a stationary population) at the 0.05 level, as illustrated by the 95 percent confidence intervals.

Risk of Extinction

The probability that the population should be classed as VULNERABLE, P_{vuln}, was significantly greater than 0 at the 0.05 level (Table 3b) under both hurricane scenarios. However, the value of P_{vuln} was 1.45 times greater with hurricanes present than its value with hurricanes absent, a difference significant at the 0.05 level. Thus, the case for classifying the RCW population as VULNERABLE was much stronger when the deleterious effects of hurricanes were included in the model.

Table 3c shows that the probability that the population is ENDANGERED, P_{endg}, was also significantly greater than 0, but very low, under both hurricane scenarios. The probability that the population is CRITICAL, P_{crit}, was negligible under either hurricane scenario (Table 3d).

Prospects for Achievement of Population Target

Table 3e shows that an OPTIMISTIC prospect for observing a population greater than or equal to the target value, $N_{trg} = 250$ breeding females, at the end of 100 years was possible (non-zero) under either hurricane scenario. However, the OPTIMISTIC prospect had a 61 percent likelihood if hurricanes were absent, but only a 12 percent likelihood if hurricanes were present. This difference was highly significant at the 0.05 level. The same pattern was apparent for the BETTER THAN EVEN CHANCE prospect for target achievement, although the

prospects differed less markedly between the hurricane scenarios (Table 3f). A PESSIMISTIC prospect of target achievement was also significantly greater than 0, and the values did not differ significantly between the hurricane scenarios (Table 3g). Note that an OPTIMISTIC prospect for target achievement was more likely than a PESSIMISTIC prospect if hurricanes were absent, while the reverse was true if hurricanes were present.

Table 3. Estimated population viability parameters in the presence vs. absence of hurricane catastrophes.*

Parameter	Hurricane Catastrophes	Parameter Estimate		Bootstrap Standard Error	Difference Normal Deviate (p-value)	Percentile 95% Confidence Limits Lower	Upper
Rate of Increase							
a) λ (yr^{-1})	Present	1.040	±	0.007	0.000	1.027	1.054
= Potential Per Capita Rate of Increase	Absent	1.040	±	0.007		1.026	1.054
Risk of Extinction							
b) P_{vuln}	Present	0.420	±	0.041	**2.390**	0.338	0.500
= Pr(VULNERABLE)	Absent	0.288	±	0.037	**(0.0168)**	0.214	0.357
c) P_{endg}	Present	0.055	±	0.019	1.017	0.019	0.097
= Pr(ENDANGERED)	Absent	0.031	±	0.014		0.006	0.058
d) P_{crit}	Present	0.000	±	0.001	0.000	0.000	0.000
= Pr(CRITICAL)	Absent		±	0.001		0.000	0.000
Prospects for Target Population Achievement							
e) P_{optm}	Present	0.126	±	0.027	**-10.267**	0.078	0.182
= Pr(OPTIMISTIC)	Absent	0.613	±	0.039	**(0.0000)**	0.539	0.688
f) P_{betv}	Present	0.536	±	0.041	**-1.997**	0.461	0.617
= Pr(BETER THAN EVEN CHANCE)	Absent	0.649	±	0.039	**(0.0458)**	0.571	0.721
g) P_{pess}	Present	0.387	±	0.041	1.270	0.305	0.468
Pr(PESSIMISTIC)	Absent	0.316	±	0.038		0.240	0.390

* Parameter estimates, bootstrap standard errors, and bootstrap percentile confidence intervals are output from PVAvES. Bias-corrected, accelerated (Bca) confidence intervals (not shown) did not differ from the percentile intervals. Normal deviates are calculated as the difference between parameters divided by the standard error of the difference. Bolded values (with associated p-values) indicate statistical significance at the 0.05 level.

Discussion

Viability of the Fort Stewart RCW population, and the Importance of Hurricanes

Hurricanes pose a serious threat to RCW recovery areas located near the Atlantic or Gulf coastlines of the eastern United States (Hooper and McAdie 1995). The present results showed that extinction risks were significantly underestimated, and prospects for achievement of long-term population goals were significantly overestimated, if hurricane catastrophes were not included in the population viability model. This suggests that PVAs performed for coastal RCW populations will likely yield the most accurate and realistic results when catastrophic effects of hurricanes are incorporated into the PVA model. Military installations listed among the RCW recovery areas most at risk from hurricanes, and to which this caveat would most likely apply are Eglin AFB, Fort Stewart, Fort Bragg, and, to a lesser degree, Fort Polk (Hooper and McAdie 1995).

The results suggest that the Fort Stewart RCW population has a substantial probability (P_{vuln} = 42% with hurricanes present) of falling into the IUCN risk class "VULNERABLE," i.e., of having at least a 10 percent chance of extinction within 100 years. This is true even though the estimated potential per capita rate of increase, λ (Table 3a) is substantially greater than 1. These results can be interpreted as either bad news or good: while P_{vuln} is significantly greater than 0, it is also significantly less than 1 at the 0.05 level (Table 3b). Further, there appears to be relatively little likelihood that the population falls into the more urgent ENDANGERED or CRITICAL risk classes, given the available data and model assumptions. The prospects for achievement of the USFWS recovery plan target population of at least 250 breeding females, at the end of 100 years, would appear to be neither strongly optimistic nor strongly pessimistic, but a pessimistic outlook is somewhat more likely.

The results presented in this report should not be taken to imply any necessity for increase in either the acreage of land managed as RCW habitat on Fort Stewart or the current recovery goals as specified in the RCW recovery plan (USFWS 1985) to compensate for the effects of hurricanes. The present results only apply to one level of carrying capacity, and do not provide any information on the overall relationship of population viability to carrying capacity. Additionally, the carrying capacity used here (506 breeding pairs) assumes the management of all uninhabited "upland" areas on the installation as RCW habitat, and so is probably very close to the upper limit of RCW carrying capacity on Fort Stewart. A more detailed report is presently in preparation by the authors (Melton, et al. Hurricanes and the Population Viability of Red-cockaded Woodpeckers

on Fort Stewart, Georgia, unpublished manuscript), in which a wider range of carrying capacities were examined. The results presented there suggest that, from a demographic point of view, little population viability would be gained by an increase in carrying capacity beyond projected levels.

Other Potential Applications of PVAvES

PVAvES is a tool for investigating the effects of potential ecological disturbances on population viability. The program allows comparison of the present state of the population with alternative, hypothetical, environmental disturbance scenarios, if the effects of disturbances can be framed as changes to the input parameters. Such alternative scenarios include: (1) catastrophic disturbances, such as hurricanes (as in the present study) and other potential catastrophes, such as infestation of RCW habitat by the southern pine beetle (e.g., Rudolph and Conner 1995); (2) natural or man-made disturbances with potential chronic effects on the population's survival and reproduction rate parameters (or their temporal variances), such as chronic noise disturbance (e.g., Delaney, et al. 1999); (3) hypothetical effects of increasing or decreasing population carrying capacity, or the rate at which carrying capacity regenerates after disturbance; (4) the effects of supplementing the population at a given annual rate through translocation of individuals from other areas, or (5) the effects of allowing a given annual rate of harvest by specifying positive or negative values for the immigration parameters (Appendix B, input 25).

Limitations of the Model

The population projection model used in this study is relatively simple in structure, incorporating only females, and using a simplified age structure (fledglings and adults). Subtleties of the RCW social structure, such as delayed reproduction and the presence of helpers at the nest, are ignored. The model assumes only a simple ceiling on the number of nesting females, and does not explicitly include population limits related to food availability. It also does not include spatial structure, or metapopulation dynamics. It assumes nothing about genetic factors, other than incorporating a pseudoextinction threshold to compensate for potential inbreeding effects at low population density.

Previous population models for the RCW (Heppel, Walters, and Crowder 1994; Maguire, Wilhere and Dong 1995; Letcher, et al. 1998) have incorporated more complex aspects of the age and social structure of RCW populations. PVAvES could, in future versions, be elaborated to incorporate more complex age and social structure. However, given only 4 years of data collection, the present model utilizes the demographic information currently available for the Fort Stewart

RCW population, thus exhibiting the virtue of being a model that the present data can support (Bessinger and Westphal 1998, Groom and Pascual 1998). The relatively simple age/stage structure of the present model allows its application to any bird species whose demography can be usefully simplified into summary statistics for average first-year and adult survival rates, and average adult fecundity rates. The input parameter estimates to PVAvES are assumed to be uncorrelated, which could potentially bias the results if there is evidence of strong correlations between life-history variables.

Lack of spatial structure is a potential source of bias in PVAvES. This is suggested by the results of Letcher et.al (1998), using an individual-based, spatially-explicit RCW population model that incorporated algorithms for within-population movement of dispersers. They found that at population sizes of 100 territories or fewer, an aggregated distribution of RCW colonies substantially reduced the number of territories lost over 100 years, relative to a dispersed colony distribution. The RCW colony sites on Fort Stewart tend to be concentrated in several training areas. The Letcher study suggests that such spatial clustering could cause the present model to somewhat overestimate probabilities of extinction on Fort Stewart.

The logistic form of the function that regenerates habitat (population carrying capacity) after catastrophes in PVAvES is also an approximation to a process (forest regeneration and ecological succession) that is actually much more complicated (e.g., James, Hess, and Kufrin 1997; Hedrick, et al. 1998 regarding RCW habitat). Carrying capacity, in PVAvES, is assumed to increase monotonically to a maximum value after being reduced by catastrophic disturbance. This may not be completely realistic: carrying capacity may naturally increase over time to a maximum and then subsequently decrease. For example, RCW habitat might follow such a pattern in the absence of management to limit the encroachment of hardwood understory into mature pine forests over time. While future versions of PVAvES may address this problem more fully, the present version should be used under the assumption of active habitat management to maximize carrying capacity of the focal species over the long run.

A positive aspect of the present model, unavailable in the previous studies, is that it incorporates information on the sampling variances associated with input life-history parameter estimates, through its use of the ASD, in its calculation of output parameter standard errors and confidence intervals. However, the large number of iterations of the generating function $g(\phi)$ necessary to this process makes the program take a long time to run (15 to18 hours for the present analyses). This is unfortunate, but necessary, if precise confidence limits for the output parameters are to be obtained. Utilization of the ASD, rather than genera-

tion of each parametric bootstrap sample directly from g(ϕ), helps to limit the iterations of g(ϕ) to a manageable number.

The IUCN extinction risk classification criteria were used as guidelines for the extinction risk classes in PVAvES. This was done because the IUCN criteria were developed explicitly to serve as objective standards for assessment of extinction risks in a wide variety of organisms because they have a well documented history of development and because they have achieved substantial international recognition. They incorporate time scales meaningful for both short term management objectives (10 – 20 years) and for predicting the longer term outlook (100 years). The risk classes calculated in PVAvES should not, however, be understood to represent a complete risk classification based on all relevant IUCN criteria. These would also include situational and historical population criteria such as recent reduction in population size or extent of occurrence, extreme population fluctuations, or population fragmentation that are not taken into account by PVAvES. Note also that the risk classes calculated in PVAvES do not use time frames based on generation length, as is specified in the IUCN risk class criteria. Generation length is calculated from the survival and reproduction rate parameters that are put into PVAvES as estimates with associated uncertainties due to sampling variance. Rather than base extinction risk classes on generation length, which can change continually during PVAvES operation, it was deemed more suitable to use non-varying time frames (10, 20, and 100 years) for the PVAvES risk class definitions.

The values used as inputs to define the proportion reduction of RCW carrying capacity and survival rate for the hurricane strength classes are admittedly somewhat speculative, being based on values recorded from only one category III hurricane event (Hurricane Hugo at Francis Marion National Forest). However, there is evidence supporting the values used for carrying capacity reduction. After the passage of Hurricane Hugo near Hobcaw Forest in South Carolina, Lipscomb and Williams (1995) report the maximum sustained wind speed recorded near Hobcaw Forest was 54 mph (87km/h) which is below the threshold for a category I hurricane. Assume that a category III hurricane wind speed of 111 mph produces a carrying capacity reduction of $\gamma_3 = 59\%$, and that habitat loss is proportional to the square of the wind speed during hurricanes (as in the present report). The predicted proportion of trees destroyed by the winds at Hobcaw would be 14%. This figure is a reasonably close approximation to the actual values for heavy timber damage at Hobcaw. Lipscomb and Williams report (see their Figure 2) that the proportion of surveyed pines showing heavy damage (bole broken, uprooted, downed) was 10% for longleaf pine, 8% for loblolly pine, and 22% for pond pine. No comparable data for the reduction of RCW survival rate at Hobcaw after Hugo were reported.

A final caveat is in order; one applicable to PVA in general. While the output statistics of model PVAvES are presented with standard errors and confidence intervals, these only indicate the range of likely output values *given the assumptions of the model.* Many parameter inputs to the model (e.g., catastrophic effects) are not incorporated with measurement or sampling error, and many effects are educated guesses, such as the value of the pseudoextinction threshold, or the maximum population carrying capacity. Furthermore, population viability models for vertebrates, by their very nature, cannot be calibrated to actual extinction data, at least on the scale of a human lifetime. The point is: results of any PVA should be taken to represent an educated guess about reality, but should not be taken to represent fact. Inferences comparing PVA results among different competing scenarios (using different input parameters), are likely to be more valid than inferences concerning the absolute viability output values for a specific set of inputs (Bessinger and Westphal 1998).

5 Summary

PVAvES is a tool for estimating the potential effects of military disturbance on the viability of endangered bird species on U.S. Army lands. Military disturbance is not addressed in this report, pending analysis of Fort Stewart training impacts data. The use of PVAvES is demonstrated by an analysis of the effects of hurricane catastrophes on the population viability of the Red-cockaded Woodpecker on Fort Stewart, GA. Hurricanes were shown to substantially increase the likelihood of extinction, and decrease the likelihood of achieving population goals, for RCW on the installation, relative to the hypothetical case in which Fort Stewart was not at risk from hurricanes. Potential uses of PVAvES related to military activities include estimating population viability effects on endangered species of : (1) "catastrophic" factors potentially causing occasional sharp increases in mortality, such as occasional years of intensified training due to political/military crises; (2) long-term (chronic) reductions of survival and/or reproduction rates due to chronic disturbances such as noise, chemicals, or changes in regular training schedules; (3) changes in population carrying capacity due to catastrophic losses of habitat (followed by regeneration) such as major fires, or more permanent habitat losses such as development of parts of the habitat for construction or other purposes; (4) population supplementation through translocation; or (5) population losses due to harvest. Some limitations of the model are discussed.

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Appendix A: Details of the PVAvES Algorithm

Let variable and subscript definitions be as in Tables 1and 2. Each time step represents 1 year.

Distributing Sampling Variability of Demographic Parameter Estimates Among Iterations

Sampling variation of demographic parameters is applied to variation of parameter values among iterations of the population viability distribution generating function, g(ϕ). Each iteration k of function g(ϕ) begins by determining the temporal mean values, for the survival and reproduction parameters, to be applied in all 1000 population runs within that iteration. A random value for the temporal mean adult survival rate, $S_{a,k..}$, is calculated as a standard beta random variable

$$S_{a,k..} = \mathrm{Beta}\{C_{ak} S_a , C_{ak} (1 - S_a)\} \tag{1}$$

where

$$C_{ak} = \{S_a (1- S_a) / \sigma_a^2\} - 1 \tag{2}$$

The use of the beta distribution restricts the range of possible values of $S_{a,k..}$ between 0 and 1, while allowing it to be distributed among iterations with mean S_a and sampling standard deviation σ_a. Analogous calculations are performed to generate random values of $S_{j,k..}$ from S_j and σ_j, and $P_{k..}$ from P and σ_P. The value for fecundity given nest success, $F_{k..}$, is calculated as

$$F_{k..} = [(F_{max} - 1) \cdot \mathrm{Beta}\{ (F - 1)/(F_{max} - 1) , \sigma_F /(F_{max} - 1) \}] + 1 \tag{3}$$

This restricts the range of $F_{k..}$ between 1 and F_{max}, while allowing $F_{k..}$ to be distributed among iterations with mean F and sampling standard deviation σ_F.

Distributing Temporal Variability of Demographic Parameter Estimates Within Runs

Temporal variation of demographic parameters is applied to variation of parameter values among time steps t, within each run j of each iteration k. The population projection model, at each time step, calculates values for survival and reproductive parameters that vary around their temporal mean values. A random value of adult survival rate for time interval t is calculated as

$$S_{a,\,kjt} = \mathrm{Beta}\{C_{at}\, S_{a,\,k..},\, C_{at}\,(1 - S_{a,\,k..})\} \tag{4}$$

where

$$C_{at} = \{\, S_{a,\,k..}\,(1 - S_{a,\,k..}) / \tau_a^2\} - 1 \tag{5}$$

This is exactly analogous to Equations 1 and 2, except that it now reflects a process variation around the temporal mean value $S_{a,\,kj\cdot}$ over time, with a temporal standard deviation τ_a. Similar calculations are used to calculate values of $S_{j,\,kjt}$ from $S_{j,\,kj\cdot}$ and τ_j, and P_{kjt} from $P_{kj\cdot}$ and τ_P. Also, the fecundity value at time t, F_{kjt}, is calculated as

$$F_{kjt} = [(F_{max} - 1) \cdot \mathrm{Beta}\{\, (F_{k..} - 1)/(F_{max} - 1)\,,\, \tau_F /(F_{max} - 1)\,\}] + 1 \tag{6}$$

in a manner analogous to Equation 3.

Dynamics of the Population Ceiling (Carrying Capacity) Within Runs

The population carrying capacity at time t, $N_{ceil,kjt}$, is determined using the formula

$$N_{ceil,kjt} = N_{max} / [\, 1 + \{(N_{max} - N_{ceil,kj(t-1)}) / N_{ceil,kj(t-1)}\} \cdot \exp(-9.91902397 / T_r)\,] \tag{7}$$

This results in a logistic growth curve for the carrying capacity over time, defined such that $N_{ceil,kjt}$, if reduced to 1 percent of its maximum value N_{max}, will increase logistically to 99 percent of N_{max}, in T_r time steps.

Application of Catastrophe Effects Within Runs

Once the survival rate and carrying capacity values for time interval t have been calculated, these values are reduced by catastrophes. Carrying capacities are reduced by a factor

$$N_{ceil,kjt} = N_{ceil,kjt} \prod_{x=1}^{10} (1-\gamma_x)^{S(x)} \tag{8}$$

Where $S(x) = Poi(\rho_x)$ is a poisson random variable with mean parameter ρ_x, independently calculated for each catastrophe level x, determining the number of catastrophes of level x that occur during time interval t. If $N_{ceil,kjt}$ is reduced below 1 percent of N_{max}, it is set equal to 1 percent of N_{max} (so that the time required to regenerate carrying capacity cannot exceed T_r). Similarly, juvenile and adult survival rates are reduced by

$$S_{a,\,kjt} = S_{a,\,kjt} \prod_{x=1}^{10} (1-\beta_x)^{S(x)} \tag{9}$$

and

$$S_{j,\,kjt} = S_{j,\,kjt} \prod_{x=1}^{10} (1-\beta_x)^{S(x)} \tag{10}$$

In the present model, survival rate reductions due to catastrophes apply only to the time interval in which the catastrophes occur, and do not carry over into the following time steps. Thus catastrophe effects on survival rates are short-term in duration, with no lingering effects in time, while catastrophe effects on carrying capacity are of relatively long-term duration, mediated by the value of T_r.

Population Projection Formulae and Demographic Stochasticity Within Runs

After implementation of catastrophe effects for the time step t, the model then projects a new breeding female population at time t+1 using the formula

$$N_{a,\,kj(t+1)} = N_{sy,\,kj(t+1)} + N_{asy,\,kj(t+1)} \tag{11}$$

Stated verbally, the new population equals the number of female fledglings surviving from the previous year ("sy" = second-year), plus the number of older females surviving from the previous year ("asy" = after-second-year). Equation 11 is calculated from the component formulas

$$N_{sy,\,kj(t+1)} = Bin(N_{hy,\,kjt}\,,\, S_{j,\,kjt}) \tag{12}$$

$$N_{hyE,\,kjt} = Bin(N_{hyfldg,\,kjt}\,,\, P_f) \tag{13}$$

$$N_{hyfldg,\,kjt} = Bin\{N_{succnest,\,kjt} \times (F_{max}-1)\,,\,(F_{kjt}-1)/(F_{max}-1)\} + N_{succnest,\,kjt} \tag{14}$$

$$N_{succnest,\,kjt} = Bin(N_{a,\,kjt}\,,\, P_{kjt}) \tag{15}$$

and

$$N_{asy,\,kj(t+1)} = Bin(N_{a,\,kjt}\,,\, S_{a,\,kjt}) \tag{16}$$

where Bin(n, p) denotes a binomial random variable with sample size n and probability parameter p.

Population Runs

Each population run consists of a series of population projections of the kind described above, starting at initial population size N_0, and proceeding for a maximum of 100 time steps. If the projected population size, $N_{a,\,kj(t+1)}$, exceeds carrying capacity, $N_{ceiling,\,kjt}$, it is set equal to this value at the end of each time step. If the projected population size takes a value less than the pseudoextinction threshold, N_{ext} , the population is considered effectively extinct, and the run is terminated at time step t. A total of 1000 runs are performed for each iteration of the population viability distribution generating function, g(ϕ).

Calculation of the Elements of y_k

The value of the potential rate of increase, λ_k , for the all runs in iteration k, is calculated as

$$\lambda_k = \{ P_{k..} \times F_{k..} \times P_f \times S_{j,k..} \} + S_{a,k} \quad (17)$$

with parameters as defined in the first section of this appendix. The value of $P_{E100,k}$ is calculated as the proportion of the 1000 population runs in iteration k that suffered pseudoextinction at a time step less than or equal to 100 steps. Similarly, the values of $P_{E20,k}$ and $P_{E10,k}$ are the proportion of runs in iteration k suffering pseudoextinction at a time step less than or equal to 20 and 10 steps, respectively. The value of $P_{N \geq target,k}$ is calculated as the proportion of runs in iteration k that have a population size greater than or equal to the target population size, N_{trg}, at the end of 100 time steps.

Calculation of the Elements of $\theta^*(b)$

After the bootstrap resampling of the ASD (see main text, Chapter 2 and Figure 1) has been completed, producing B bootstrap sub-samples, a bootstrap population viability parameter vector, $\theta^*(b)$, is calculated for each bootstrap sub-sample b. The value of $\lambda^*(b)$ is calculated as the mean value of λ^*_n among the N elements within sub-sample b. The value of $P_{vuln}^*(b)$ is calculated as the proportion of the N elements of sub-sample b that had values of $P^*_{E100,n}$ greater than or equal to 0.1, the IUCN threshold for classification as VULNERABLE. Similarly, the value of $P_{endg}^*(b)$ is the proportion of the N elements that have values of $P^*_{E20,n}$ greater than or equal to 0.2, the IUCN threshold for ENDANGERED, and $P_{crit}^*(b)$ is the proportion that had values of $P^*_{E10,n}$ greater than or equal to 0.5, the IUCN threshold for CRITICAL. The values of $P_{optm}^*(b)$, $P_{btev}^*(b)$, and $P_{pess}^*(b)$ are calculated as the proportion of the N elements of sub-sample b that have values of $P^*_{N \geq target,k}$ that are greater than 0.9, greater than 0.5, or less than 0.1, respectively.

Appendix B: Data File

Following is a printout of the formatted input data file used in this study for the "Hurricane Catastrophes Present" scenario. The input file for the "Hurricane Catastrophes Absent" scenario was exactly the same, except that the value for input #27 was set to equal 0, rather than 1.

```
********************************************************
************                                ************
************ INPUT DATA FOR PROGRAM PVAvES ************
************                                ************
********************************************************


*********************************
*** INITIALIZATION PARAMETERS ***
*********************************

 1) Seed1 =                                              123456

 2) Seed2 =                                              765432

 3) Effective Sample Size from Demographic Data =           154

 4) Number of Bootstrap Iterations =                       2000

 5) Size of Approximated Sampling Distribution =          10000

 6) Coverage of Confidence Intervals =                     0.95

*******************************************
*** POPULATION AND THRESHOLD PARAMETERS ***
*******************************************

 7) Initial population size =                                  140
    (breeding females)

 8) Maximum population carrying capacity =                     506
   (breeding females, in the absence of catastrophes)

 9) Extinction threshold =                                       5

10) Target population size after 100 years =                   250


******************************
*** DEMOGRAPHIC PARAMETERS ***
******************************

11) Mean proportion of successful nests =                                      0.8111
12)   with temporal standard deviation =                                       0.0000
13)   and sampling standard deviation =                                        0.0629

14) Mean seasonal fecundity of successful nests (fledglings of both sexes) = 2.0905
15)   with temporal standard deviation =                                       0.0334
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```
16)   and sampling standard deviation =                                   0.1344

17) Maximum possible seasonal fecundity =                                 4
    (fledglings of both sexes)

18) Probability that a fledgling is female =                              0.5
    (based on fledgling sex ratio)

19) Mean fledgling female survival rate (to next breeding season) =       0.3901
20)   with temporal standard deviation =                                  0.0000
21)   and sampling standard deviation =                                   0.0624

22) Mean adult female annual survival rate =                              0.7092
23)  with temporal standard deviation =                                   0.0402
24)  and sampling standard deviation =                                    0.0572


******************************
*** IMMIGRATION PARAMETERS ***
******************************

25) Immigration constant or stochastic (poisson)?  =          0
    (Enter 0 for CONSTANT, 1 for STOCHASTIC )

26) Mean immigration rate (breeding females per year) =        0
    (must be an integer for CONSTANT immigration)



**********************************************
** HURRICANE CATASTROPHE PARAMETER VALUES ***
**********************************************

27) Catastrophes are included in model, and reduce annual survival rates? =
    1  (Enter 0 or 1: 0 for NO, 1 for YES)

28) Catastrophes also reduce carrying capacity? = 1
    (Enter 0 or 1: 0 for NO, 1 for YES)

29) Regeneration time of carrying capacity (years) = 100
    (Time for carrying capacity to grow from 1% to 99% of its maximum value)

Category 1 Catastrophes:
30)    Rate of occurrence (annual) =                   0.04
31)    Proportional reduction in survival rates =      0.28
32)    Proportional reduction in carrying capacity = 0.2622

Category 2 Catastrophes:
33)    Rate of occurrence (annual) =                   0.0091
34)    Proportional reduction in survival rates =      0.4712
35)    Proportional reduction in carrying capacity = 0.4413

Category 3 Catastrophes:
36)    Rate of occurrence (annual) =                   0.0035
37)    Proportional reduction in survival rates =      0.63
38)    Proportional reduction in carrying capacity = 0.59

Category 4 Catastrophes:
39)    Rate of occurrence (annual) =                   0.0000
40)    Proportional reduction in survival rates =      0.0000
41)    Proportional reduction in carrying capacity = 0.0000

Category 5 Catastrophes:
42)    Rate of occurrence (annual) =                   0.0000
43)    Proportional reduction in survival rates =      0.0000
44)    Proportional reduction in carrying capacity = 0.0000

Category 6 Catastrophes:
45)    Rate of occurrence (annual) =                   0.0000
46)    Proportional reduction in survival rates =      0.0000
47)    Proportional reduction in carrying capacity = 0.0000
```

```
Category 7 Catastrophes:
48)   Rate of occurrence (annual) =                   0.0000
49)   Proportional reduction in survival rates =      0.0000
50)   Proportional reduction in carrying capacity = 0.0000

Category 8 Catastrophes:
51)   Rate of occurrence (annual) =                   0.0000
52)   Proportional reduction in survival rates =      0.0000
53)   Proportional reduction in carrying capacity = 0.0000

Category 9 Catastrophes:
54)   Rate of occurrence (annual) =                   0.0000
55)   Proportional reduction in survival rates =      0.0000
56)   Proportional reduction in carrying capacity = 0.0000

Category 10 Catastrophes:
57)   Rate of occurrence (annual) =                   0.0000
58)   Proportional reduction in survival rates =      0.0000
59)   Proportional reduction in carrying capacity = 0.0000
```

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14. ABSTRACT
This report presents version 1.0 of the Population Viability for Avian Endangered Species (PVAvES) computer model. The program is designed to assess the viability of endangered bird species populations on U.S. Army lands. It also facilitates the comparison of alternative ecological scenarios based on different assumptions about the effects of natural or human (military) activities. The primary algorithms used in PVAvES are described.

The model is used to assess the viability of the Red-cockaded Woodpecker (RCW) *Picoides borealis*, population at Fort Stewart, GA. The results showed that extinction risks were significantly underestimated, and prospects for achievement of long-term population goals were significantly overestimated, if hurricane catastrophes were not included in the population viability model. This suggests that the effects of hurricanes should not be ignored in future population viability analysis of coastal RCW populations.

Some potential uses of PVAvES include estimating population viability effects of: (1) ecological catastrophes, (2) long-term (chronic) ecological disturbance of survival and/or reproduction rates, (3) changes in population carrying capacity regenerates after disturbance, (4) population supplementation through translocation, or (5) population losses due to "take." Some limitations of the model are discussed.

15. SUBJECT TERMS
endangered species, birds, population viability analysis (PVA), natural resource management, carrying capacity, computer programs, PVAvES

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